

Quantifying male attractiveness

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Genetic models of sexual selection are concerned with a dynamic process in which female preference and male trait values coevolve. We present a rigorous method for characterizing evolutionary endpoints of this process in phenotypic terms. In our phenotypic characterization the mate-choice strategy of female population members determines how attractive females should find each male, and a population is evolutionarily stable if population members are actually behaving in this way. This provides a justification of phenotypic explanations of sexual selection and the insights into sexual selection that they provide. Furthermore, the phenotypic approach also has enormous advantages over a genetic approach when computing evolutionarily stable mate-choice strategies, especially when strategies are allowed to be complex time-dependent preference rules. For simplicity and clarity our analysis deals with haploid mate-choice genetics and a male trait that is inherited phenotypically, for example by vertical cultural transmission. The method is, however, easily extendible to other cases. An example illustrates that the sexy son phenomenon can occur when there is phenotypic inheritance of the male trait.

Keywords: Fisher process; sexual selection; sexy son; mate choice; evolutionarily stable strategy; phenotypic models

1. INTRODUCTION

It is only adaptive for females to be selective about their choice of mate if males differ in their value to a female. A male's value as a mate may depend on direct or indirect benefits (Kirkpatrick & Ryan 1991; Kokko *et al.* 2003). Direct benefits are advantages such as food, protection or a good territory that a male may provide for a female or her young. Indirect benefits are based on a male's genes. The genes that a male passes on to its offspring may influence the offspring's ability to survive and reproduce. One way in which genes may influence offspring reproductive success is by determining the attractiveness of male offspring to females. This effect was proposed by Fisher (1930) as the basis for an explanation of exaggerated male traits.

Fisher argued that, given an initial female preference for a male trait, both the strength of the female preference and the value of the male trait could be increased by sexual selection. The male trait is favoured because of the female preference, and the female trait is favoured because females that are choosy have sons that are preferred. Fisher gave a verbal account of this 'runaway process'. Lande (1981) and Kirkpatrick (1982) constructed models based on population genetics to show that Fisher's runaway process could work. In these models, the female does not incur any cost as a result of being choosy. Pomiankowski (1987) showed in a particular context that including costs of female preference resulted in no permanent effect

of the Fisher process. Subsequent work demonstrated that the Fisher process could still occur if the genes controlling the male trait were subject to biased mutation (Pomiankowski *et al.* 1991).

The basis of the Fisher process is that it is more valuable for a female to mate with some males than with others. This advantage might be able to compensate for any direct disadvantage associated with choosing a male as a mate. For example, if males differ in both attractiveness and the care that they provide for their offspring, then it might be advantageous for a female to mate with an attractive male even if he provides less care than an unattractive male. This idea is known as the sexy son hypothesis (Weatherhead & Robertson 1979) because females are compensated for reduced male care by having sexy sons. Weatherhead and Robertson supported their idea with a simple model based on counting descendants a given number of generations into the future. Kirkpatrick (1985) pointed out that the model of Weatherhead and Robertson was incorrect. He also argued more generally that the procedure of counting descendants was not valid (see also Arnold 1983). From his genetic analysis, Kirkpatrick concluded that the advantage of sexy sons could not compensate a female for a direct cost, but Pomiankowski *et al.* (1991) showed that the sexy son effect can occur in some genetic models.

We can explain the Fisher process in terms of the value to a female of mating with different males. In contrast to this perspective, models based on genetics deal with the change of gene frequencies over time, rather than ideas of value. Genetic models have done much to further our understanding of sexual selection, but it can be argued that they lack the intuitive appeal of phenotypic expla-

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nations based on values and rewards. The genetic approach is clearly fundamental. Does this mean that the intuitive arguments based on value are sloppy, or can they be made precise in the sense that they give the same final outcomes as a genetic analysis? If phenotypic explanations cannot be made precise then the intuition afforded by verbal arguments may be misleading. Conversely, if they can be made precise, then careful verbal arguments based on a suitable idea of value provide considerable advantages. It can be difficult to analyse the evolution of a large number of traits in a genetic model. The conversion to a phenotypic model makes it possible to characterize endpoints in terms of game theory or optimality and hence makes the analysis much easier. More importantly, the phenotypic approach offers genuine insight into sexual selection (Grafen 1990a,b; Pen & Weissing 2000; Kokko *et al.* 2002).

Taylor (1990) develops a technique that can be used to translate genetic models into phenotypic models using reproductive value. Pen & Weissing (2000) use this technique to give a phenotypic account of mate choice and sexual selection. In this paper we present an alternative technique that gives the same end result as the analysis of Taylor (1990), but achieves this result more directly in the case we analyse. Our phenotypic account is similar to that of Pen & Weissing (2000) but is applied to a different aspect of sexual selection. We consider a simple model in which females choose the male that they will mate with on the basis of the value of a male's trait. A female's rule for choosing a mate is genetically determined by a single haploid locus. For simplicity we assume that the trait of a male is determined, with error, by the trait of his father, i.e. transmission is based on phenotype rather than genotype. This paternal effect could be based on vertical cultural inheritance, such as inheritance of song in some species of bird or the inheritance of wealth in humans. (It could also be transmitted on a chromosome that only occurs in males.) For this model we show that the endpoints of selection can be characterized phenotypically in a rigorous way. The heart of our analysis involves assigning an attractiveness to a male that quantifies the advantage to a female of mating with the male. This value is not assumed in advance; instead it emerges in a self-consistent way from our analysis.

We have deliberately chosen a context in which the logic of our approach can be clearly demonstrated. Both diploid determination of the mate-choice rule and genetic inheritance of the male trait introduce complications that are described in the discussion. Despite these complications, our approach can still be used to obtain a phenotypic account in these cases.

2. THE MODEL

We consider a large, well mixed, sexually reproducing population. Males are of one of K distinct phenotypes labelled $1, \dots, K$. Type is passed (with error) from father to son phenotypically. There is an annual breeding season in which each female chooses which male or males to mate with. Offspring that result from matings in one breeding season are sexually mature by the next breeding season. A female's mate-choice rule determines what types of males the female prefers to mate with and how choosy she

is. Typically choosiness incurs costs. For example, a choosy female might tend to take longer to find a mate and hence leave fewer surviving offspring, either because she is in poorer condition at reproduction or because young produced late have lower survival prospects. The female's mate-choice rule may also affect the probability that she survives to breed again next year. We assume, however, that the mate-choice rule used by a female does not affect her before her first breeding season.

A female's mate-choice rule is determined by a single haploid autosomal locus. Alleles are denoted by π, π' , etc. We assume a one-to-one correspondence between possible mate-choice rules and alleles. Thus for every mate-choice rule there is a unique allele that codes for this rule. Given this assumption we simplify notation, allowing π to denote an allele and the mate-choice rule that is coded for by the allele. A male carries, but does not express, the mate-choice allele that it inherits from its parents. Each offspring inherits the mate-choice allele of its mother with probability 0.5 and that of its father with probability 0.5.

(a) *Invasibility and evolutionary stability*

We will say that strategy π is the resident mate-choice strategy if all population members are genetically π . Consider a population where π is the resident strategy. Let this population be demographically stable, i.e. the population has stable growth (or constant size, if density-dependent effects are acting) and has a stable composition over time. In particular, the sex ratio is stable, as are the proportions of males of each type. Suppose that a mutant π' allele arises in this resident π population. Will the mutant invade into the resident population? If the mutation arises just once, then it may become extinct because of demographic stochasticity, even if the mutation confers high fitness. We ignore such chance events and focus on mutations that are not too rare. Then invasion is concerned with whether mean mutant numbers grow faster than resident numbers when mutant numbers are still rare compared with residents.

To quantify the rate of growth of mutant numbers we census the population annually at the start of each breeding season. At a census time a π' allele can be in one of $K + 1$ types of individual; a female or a type j male, $j = 1, \dots, K$. First consider a π' female present at the start of a breeding season. The π' descendants of this female that are present at the start of the breeding season next year comprise: (i) any π' offspring produced this year that survive until next year; and (ii) the female herself, if she survives. We enumerate such descendants by the functions

$\alpha_i(\pi', \pi)$ = expected number of π' type i male descendants left next year.

$\beta(\pi', \pi)$ = expected number of π' female descendants left next year.

Now consider a π' type j male present at the start of a breeding season. His π' descendants are enumerated by the functions

$a_{ij}(\pi)$ = expected number of π' type i male descendants left next year.

$b_j(\pi)$ = expected number of π' female descendants left next year.

These quantities depend on π but not π' because of the following assumptions: (i) the mate-choice gene is not expressed in males; (ii) a π' male will almost certainly mate with a π female because the π' allele is rare; and (iii) daughters are not affected by the mate-choice allele that they carry until their first breeding season; sons are also not affected.

Suppose that in year t there are $n_j(t)$ π' type j males and $n_f(t)$ π' females present at the start of the breeding season. Then, provided numbers of the π' allele are not too small (so that demographic stochasticity can be ignored), numbers present in year $t + 1$ are related to numbers present in year t by $\mathbf{n}^T(t + 1) = \mathbf{L}(\pi', \pi) \mathbf{n}^T(t)$, where $\mathbf{n}^T(t)$ is the transpose of the row vector $\mathbf{n}(t) = (n_1(t), n_2(t), \dots, n_K(t), n_f(t))$ and $\mathbf{L}(\pi', \pi)$ is the $(K + 1)$ by $(K + 1)$ matrix

$$\mathbf{L}(\pi', \pi) = \begin{pmatrix} a_{11}(\pi) & a_{12}(\pi) & \dots & a_{1K}(\pi) & \alpha_1(\pi', \pi) \\ a_{21}(\pi) & \dots & \dots & a_{2K}(\pi) & \alpha_2(\pi', \pi) \\ \vdots & & & \vdots & \vdots \\ a_{K1}(\pi) & \dots & \dots & a_{KK}(\pi) & \alpha_K(\pi', \pi) \\ b_1(\pi) & \dots & \dots & b_K(\pi) & \beta(\pi', \pi) \end{pmatrix}. \quad (2.1)$$

We refer to $\mathbf{L}(\pi', \pi)$ as the projection matrix for the π' allele when the resident strategy is π . Over time, the annual proportionate increase in the total number of mutant alleles will settle down:

$$\frac{\text{total mutant numbers in year } t + 1}{\text{total mutant numbers in year } t} \rightarrow \lambda(\pi', \pi), \quad (2.2)$$

where the stable growth rate $\lambda(\pi', \pi)$ is the maximum eigenvalue of the projection matrix $\mathbf{L}(\pi', \pi)$. Following Metz *et al.* (1992) we assume that the resident strategy π is stable against invasion by the mutant allele π' if

$$\lambda(\pi', \pi) < \lambda(\pi, \pi), \quad (2.3)$$

that is, within the resident π population the growth rate of mutant allele numbers is less than that of resident allele numbers. This invasion criterion does not just count children or grandchildren. Instead, by using stable growth rates it counts the number of copies of itself that an allele leaves far into the future.

A resident strategy π^* is an evolutionarily stable strategy (ESS) if no strategy different from π^* can invade (Maynard Smith 1982). Thus a sufficient condition for π^* to be an ESS is that

$$\lambda(\pi, \pi^*) < \lambda(\pi^*, \pi^*) \quad \text{for all } \pi \neq \pi^*. \quad (2.4)$$

In other words, if we regard $\lambda(\pi', \pi)$ as the payoff to the strategy π' playing against the strategy π in a game, then a sufficient condition for the evolutionary stability of a mate-choice strategy π^* is that π^* is the unique best response to itself in this genetic game. We now introduce a phenotypic game whose equilibrium solutions coincide with those of this game.

(b) The phenotypic game

Suppose that all population members are genetically π , that is π is the resident mate-choice strategy, then the population projection matrix is $\mathbf{L}(\pi, \pi)$. Let the vector $\mathbf{V}(\pi) = (V_1(\pi), V_2(\pi), \dots, V_K(\pi), 1)$ be the eigenvector of $\mathbf{L}(\pi, \pi)$ satisfying

$$\mathbf{V}(\pi) \mathbf{L}(\pi, \pi) = \lambda(\pi, \pi) \mathbf{V}(\pi). \quad (2.5)$$

Then $V_j(\pi)$ is the reproductive value of a type j male relative to a female. This is the ratio of the expected number of descendants left at some time far in the future by the male relative to the expected number left by a female at this time (e.g. Houston & McNamara 1999; Caswell 2001).

We now use reproductive value to construct the payoff in another game. For strategies π' and π set

$$W(\pi', \pi) = \sum_{i=1}^K \alpha_i(\pi', \pi) V_i(\pi) + \beta(\pi', \pi). \quad (2.6)$$

We refer to the game with payoff W as the phenotypic game. $W(\pi', \pi)$ is the expected total reproductive value of the offspring left next year by a female using mate-choice strategy π' , where reproductive value is that under the resident strategy π .

In Appendix A it is shown that the genetic and phenotypic game payoffs are related by

$$W(\pi', \pi) < W(\pi, \pi) \Leftrightarrow \lambda(\pi', \pi) < \lambda(\pi, \pi). \quad (2.7)$$

The left-hand inequality says that a mutant female which uses mate-choice strategy π' this year, but whose descendants revert to the resident mate-choice strategy π in future years, will leave fewer descendants far in the future than a resident female. As relationship (2.7) shows, this is equivalent to the mutant leaving fewer descendants if all her descendants use strategy π' rather than reverting to π .

Relationship (2.7) allows us to reformulate the conditions for the evolutionary stability of a strategy π^* in terms of W rather than λ . By criterion (2.4) and result (2.7) a sufficient condition for π^* to be an ESS is that

$$W(\pi', \pi^*) < W(\pi^*, \pi^*) \quad \text{for all } \pi' \neq \pi^*. \quad (2.8)$$

In the language of game theory, if a strategy π^* is the unique best response to itself in the genetic game it is the unique best response to itself in the phenotypic game. (This does not mean that the two games have the same best response functions; in general they do not.) The characterization of evolutionary stability given by expression (2.8) can also be obtained using the method given by Taylor (1990).

For the specific mate-choice model we present below, every strategy has a unique best response. That is, for every strategy π there is a unique strategy $B(\pi)$ such that

$$W(B(\pi), \pi) = \max_{\pi'} W(\pi', \pi). \quad (2.9)$$

Thus, in this case a strategy π^* is an ESS if and only if

$$B(\pi^*) = \pi^*. \quad (2.10)$$

3. EXAMPLE: MALES ENCOUNTERED AS A POISSON PROCESS

To illustrate the above theoretical results we specify a detailed model of the mate-choice process. Assume non-overlapping generations with a generation time of 1 year. The annual breeding season starts at time of year $t = 0$ and ends at time $t = T_{\text{season}}$. During a breeding season a female searches until she finds a suitable mate. While searching she encounters males as a Poisson process of rate unity.

Encountered males are drawn at random from the population. On each encounter the female must decide whether to mate with that particular male, or reject him and continue to search. On mating she stops searching, produces offspring and then dies. If she has not mated by the end of the breeding season she dies without producing any offspring. A male may mate with many females during a season. After the breeding season he also dies.

Mating with a type i male produces, on average, N_i offspring, of which half are sons and half are daughters. Survival of offspring to maturity is independent of their sex and type. It is also independent of the time at which the parents mated. Thus the only cost to the female of rejecting a male is that she may not encounter another before the end of the breeding season, and hence may fail to breed.

Define $r_i(\pi)$ to be the expected total reproductive value of the surviving offspring if a female mates with a type i male. We refer to $r_i(\pi)$ as the attractiveness of a type i male. By equations (2.6) and (2.9), a female following the best response strategy $B(\pi)$ maximizes the expected attractiveness of the male that she chooses. This strategy can thus be found by standard dynamic optimization techniques (e.g. Whittle 1982). Because an ESS is the best response to itself, in an evolutionarily stable population the attractiveness of a type i male describes the strength of preference of resident females for a male of this type.

Whatever the resident mate-choice strategy, it can be shown that the best response is uniquely defined and has the following form determined by the K switch times t_1, t_2, \dots, t_K . On encountering a type i male at time t a searching female rejects the male if $t < t_i$ and mates with the male if $t \geq t_i$.

(a) *Two male types*

Suppose that there are two types of males (i.e. $K = 2$) and that among the sons of a type i male a proportion $1 - p_i$ are type i and a proportion p_i are the other type. We refer to p_1 and p_2 as mutation rates because they specify the error in passing on type from father to son. To obtain a positive correlation between son's type and father's type we assume that $p_1 + p_2 < 1$. Note that, given the assumptions of the model, the absolute values of N_1 and N_2 are not relevant, only their ratio N_1/N_2 affects results.

At least one of the switch times t_1 and t_2 is zero because it is never optimal for a female to reject both types of male at time 0. Because best responses are of this form, in searching for an ESS we can restrict attention to resident strategies of this form. In other words, we restrict attention to strategies π that can be expressed as a pair of non-negative numbers $\pi = (t_1, t_2)$, where at least one of these numbers is zero.

(i) *Symmetric case*

Consider the case where $N_1 = N_2$ and $p_1 = p_2$. Then the two males are identical, except for a label that is recognized by females. In this case the mate-choice strategy of taking the first male encountered (i.e. the strategy $\pi^* = (0, 0)$) is always an ESS (and always continuously stable; see below). We refer to this strategy as one of no preference. When presenting results we show this ESS and those where females prefer type 1 males, i.e. ESSs of the form $\pi^* = (0, t_2^*)$, where $t_2^* > 0$. By symmetry, whenever

such an ESS exists there is a mirror image ESS with preference for type 2 males, and vice versa.

A female that follows mate-choice strategy $\pi = (0, t_2)$ always accepts type 1 males. The larger the switch time t_2 , the more costs she is prepared to incur to obtain a type 1 male rather than a type 2 male. In other words, as t_2 increases so does her strength of preference for type 1 males. An increase in the preference of resident females for type 1 males increases the number of matings of the sons, grandsons and so on, of type 1 males. Thus it increases the advantage to a mutant female of mating with a type 1 male rather than a type 2 male. This advantage, quantified as relative attractiveness, is illustrated in figure 1a.

In this symmetric case, when resident females prefer type 1 males, the best response of a mutant female is either to show no preference or to show a preference for type 1 males as well. With a slight abuse of notation we denote the best response to the resident mate-choice strategy $\pi = (0, t_2)$ by $B(\pi) = (0, B(t_2))$. Figure 1b illustrates best response functions.

A resident strategy $\pi^* = (0, t_2^*)$ is an ESS if and only if $B(t_2^*) = t_2^*$. This criterion means that no mutant following another strategy can invade into a population where the resident strategy is already π^* . Another stability criterion is that of continuous stability (Eshel 1983). A population is continuously stable if it will evolve to π^* when initially displaced slightly from π^* . Let the resident mate-choice strategy be $\pi = (0, t_2)$. If $B(t_2) > t_2$, then a female following the best mutant strategy has a stronger preference for type 1 males than resident females. Under suitable regularity conditions (see Appendix B) this means that the population will evolve towards higher preference. Conversely, if $B(t_2) < t_2$, the population will evolve towards less preference. Thus for the special one-dimensional case we are considering, an ESS $\pi^* = (0, t_2^*)$ is also continuously stable if the slope of B satisfies $B'(t_2^*) < 1$ (cf. Eshel 1983; Taylor 1989). Conversely, if $B'(t_2^*) > 1$, then a population displaced from π^* in either direction will evolve further away from π^* in that direction, so that π^* is situated on an invasion barrier. It is reasonable to suppose that an endpoint of the process of evolution is both an ESS and continuously stable; i.e. it is a CSS as defined by Eshel.

Figure 1b illustrates the best response to the resident mate-choice strategy for two values of the common mutation probability. For each value, when resident females have a weak preference for type 1 males, the best response is to have no preference. A population where initially females had a weak preference for type 1 males would thus evolve to no preference. When the mutation probability is high, females following the best response strategy always have a weaker preference for type 1 males than resident females. Thus the only ESS is one of no preference. When the mutation probability is low, females following the best response strategy have a greater preference for type 1 males than resident females for a range of resident mate-choice strategies. There are then three ESSs, but the middle one is not continuously stable and forms an invasion barrier between the other two.

Figure 2 shows the effect of breeding season length. When the season is short a female cannot afford to be choosy and no preference is the only ESS. For longer season length there is less likelihood that a female who rejects

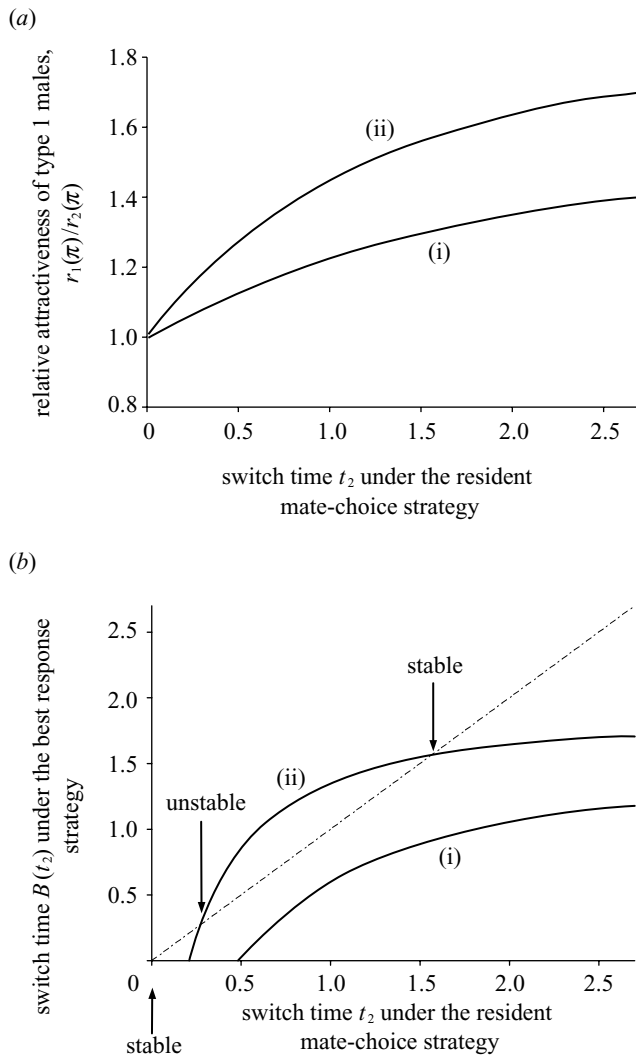


Figure 1. The effect of the resident mate-choice strategy when there is symmetry between the two types of male. The resident strategy is $\pi = (0, t_2)$, indicating that type 1 males are always accepted and type 2 males are rejected before the switch time t_2 . (a) The attractiveness of type 1 males relative to type 2 males, $r_1(\pi)/r_2(\pi)$. (b) The best response $B(\pi) = (0, B(t_2))$ to the resident strategy. For case (ii), arrows mark the three solutions of the equation $B(t_2^*) = t_2^*$, and it is also indicated whether or not each ESS is continuously stable. Cases are (i) high mutation probabilities $p_1 = p_2 = 0.3$; (ii) low mutation probability $p_1 = p_2 = 0.15$. $T_{\text{season}} = 2.7$, $N_1 = N_2$.

a type 2 male early in the season will fail to encounter another male. Thus the female loses little by being choosy, and there are also two other ESSs, one of which is continuously stable whilst the other is not. As in figure 1, the continuously stable ESS is separated from the no-preference ESS by the invasion barrier formed by the other ESS (figure 2a). As the season length increases, and hence the cost of being choosy decreases, the relative attractiveness of type 1 males at the choosy ESS increases (figure 2b).

(ii) Effect of N_1/N_2

We now allow the two types of male to produce different numbers of offspring. Figure 3 shows how the continuously stable ESSs and invasion barriers depend on the

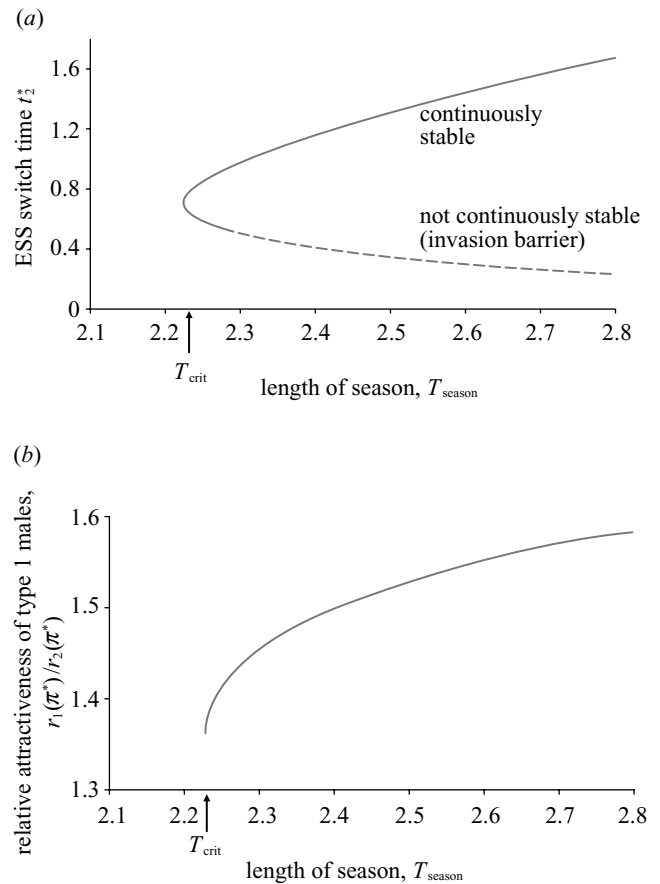


Figure 2. The effect of the length of the breeding season T_{season} when there are two male types. (a) ESS mate-choice rules of the form $\pi^* = (0, t_2^*)$. For $T_{\text{season}} < T_{\text{crit}}$ no preference is the only ESS. For $T_{\text{season}} > T_{\text{crit}}$ a second continuously stable ESS is separated from the no-preference ESS by an invasion barrier. (b) The attractiveness of type 1 males relative to type 2 males at the continuously stable ESS with preference for type 1 males. $p_1 = p_2 = 0.15$, $N_1 = N_2$.

ratio N_1/N_2 . As can be seen, for a range of values of N_1 and N_2 with $N_1 < N_2$ there is a continuously stable ESS with preference for type 1 males. In other words, at evolutionary stability females prefer males that produce less offspring. This is an example of the sexy son phenomenon (Weatherhead & Robertson 1979).

(b) Multiple male types

Figure 4 presents results for an example in which there are 50 types of male. In this example the number of surviving offspring that result from mating with a type i male decreases as i increases (figure 4a). The mean type of the sons of a type i male lies between 1 and i , so that mutation is biased and tends to reduce type number (cf. Iwasa *et al.* 1991; Pomiankowski *et al.* 1991). Full details on the number and type of offspring are given in Appendix C. The figure shows aspects of the resident population at each of two continuously stable ESSs. Computations (examining sensitivity to initial conditions) suggest that these are the only continuously stable ESSs. At one ESS females prefer males that provide the most offspring. At the other, females prefer males of intermediate type to males that produce the most offspring and to males that produce very few. This is a further example of the sexy son phenomenon.

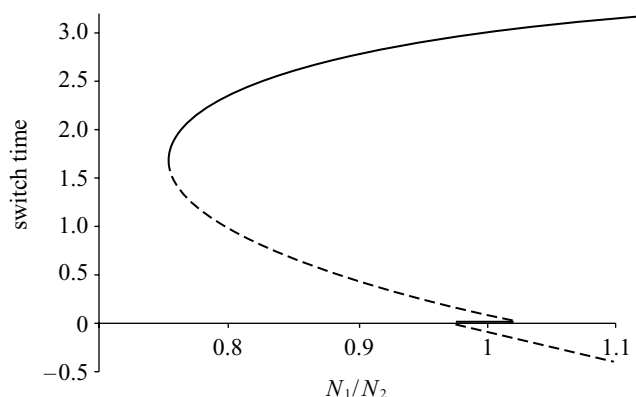


Figure 3. The effect of the number of surviving offspring on the number and stability of ESSs that are present. There are two types of male, so that results depend on the ratio N_1/N_2 . Continuously stable ESSs lie on the solid lines; invasion barriers lie on dashed lines. In showing ESSs we adopt the following convention: a positive switch time t corresponds to the ESS $(0, t)$ with preference for type 1 males; a negative switch time $-t$ corresponds to the ESS $(t, 0)$ with preference for type 2 males. Only a small range of negative values is shown, but the full curve can be constructed by symmetry with the positive values. $p_1 = p_2 = 0.15$, $T_{\text{season}} = 4$.

4. DISCUSSION

We have shown that the Fisher process and the sexy son effect can occur when the female trait is genetically determined and the male trait is culturally determined and inherited by vertical transmission. Although there have been previous models of cultural transmission and sexual selection (e.g. Laland 1994a,b; Aoki *et al.* 2001; Nakajima & Aoki 2002), this particular issue has not been addressed.

Any model that analyses the Fisher process, or, more generally, mate choice for indirect benefits, cannot just count offspring number because the beneficial effects of choosing a sexy son do not begin to appear until grandchildren are produced. In contrast to approximations that look no further into the future than grandchildren (Weatherhead & Robertson 1979; Heisler 1981), our approach looks at the asymptotic rate of spread of a mate-choice allele. We then translate results on spread rates into results about the total reproductive value of descendants left in 1 year's time. In this way, structuring the population and allowing reproductive value to depend on type, we are able to look just 1 year into the future in assessing whether a mutant allele can ultimately invade. This equivalence of the long-term and short-term fitness advantage has been pioneered by Taylor (1990) in the context of translating genetic models into phenotypic models. Our analysis in this specific case is more direct than that of Taylor, but reaches the same conclusion.

A further benefit of our method is that we do not need to make the assumption of fixed correlations between traits and preferences. Genetic approaches need to consider the correlation between the female mate-choice allele carried by a male and male's trait value, but are unable to generate this correlation from first principles except in cases of very few loci (e.g. Kirkpatrick 1982). Our approach obviates the need to look at correlations because counting numbers of offspring of each type, rather than

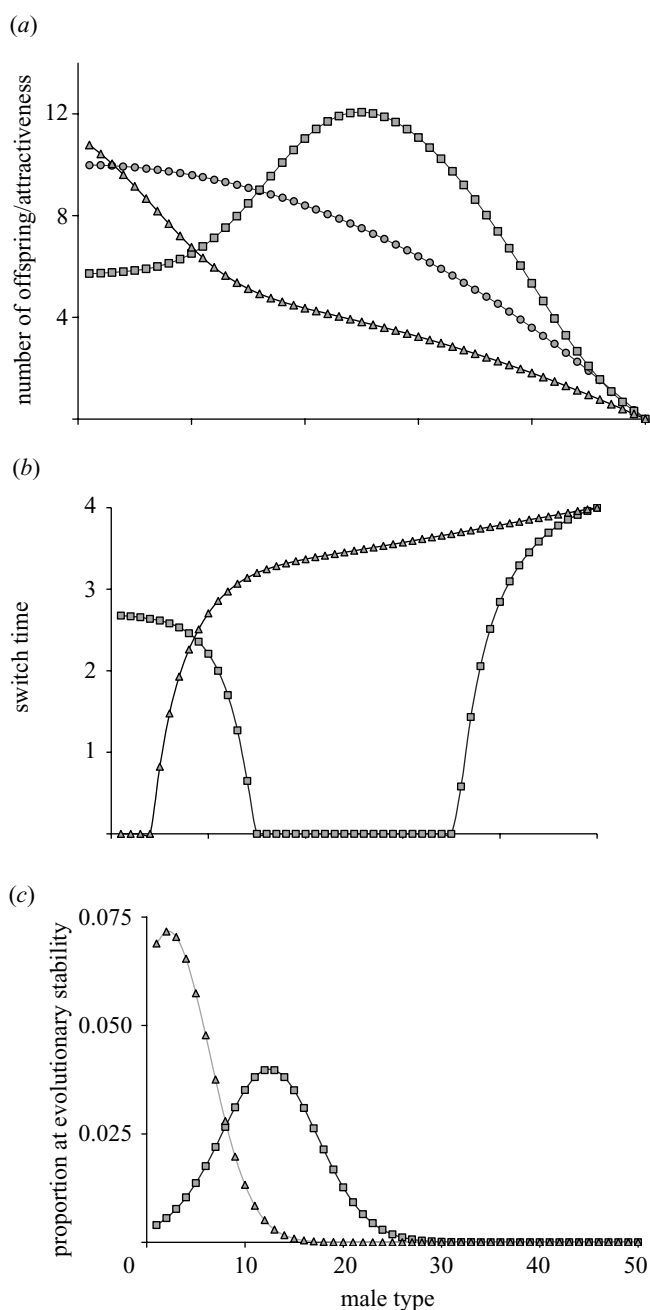


Figure 4. Example with 50 types of male. Two ESSs, referred to as ESS1 and ESS2, are illustrated. (a) For each male type: the number of surviving offspring left by a female if she mates with a male of this type (the N_i of the text), and the attractiveness of a male of this type at each ESS. Circles, offspring number; squares, attractiveness ESS2; triangles, attractiveness ESS1. (b) The two ESS mate-choice strategies, each specified by a sequence of switch times t_1, t_2, \dots, t_{50} . Squares, switch times ESS2; triangles, switch times ESS1. (c) The proportion of males of each type at each of the ESSs. Squares, proportion ESS2; triangles, proportion ESS1. $T_{\text{season}} = 4$.

just total numbers, automatically takes correlation into account. In other words, a female with a preference is more likely to have her offspring sired by an attractive male, which automatically establishes a correlation between female preferences and offspring traits when both the trait and the preference is passed on to offspring.

Pen & Weissing (2000) analyse a specific model of sexual selection using an approach based on that of Taylor (1990). In their model, males inherit the propensity y to develop into a particular type, and any correlation between the type of a father and that of his son is solely due to inheritance of this y value. Thus if population members all have the same y values (for example, at evolutionary stability) then there is no correlation between father's type and son's type. Pen & Weissing (2000) conclude that when female preference is costly there is no stable equilibrium with female preference for sexy sons. They thus infer that Fisherian runaway models are most relevant when female preference pre-exists for some reason not included in the model. By contrast, our analysis, which incorporates a positive correlation between the type of a father and that of his sons (even at evolutionary stability), shows that simple models can predict stable equilibria with female preference for sexy sons. Generally, for a sexy son benefit to cause the evolution of female choice despite direct costs that it incurs, it appears necessary that there is a process that maintains variation in offspring sexiness, despite the directional selection provided by female preference (Kokko *et al.* (2002); 'handicap' version of the model of Pomiankowski *et al.* (1991), Eshel *et al.* (2000)). Models that lack this assumption do not predict stable female choice (Kirkpatrick (1985), Pomiankowski (1987); 'large-effect mutation' version of the model of Eshel *et al.* (2000)). In our model, this variation is provided by errors in transmission from father to son.

Our approach characterizes the stable endpoints of the evolutionary process in phenotypic terms (cf. Grafen 1990a; Taylor 1990; Eshel 1996; Hammerstein 1996; Weissing 1996; Pen & Weissing 2000). This approach gives us a consistent way to measure the 'costs' and 'benefits' of mating with a particular male, when fitness consequences include direct as well as indirect effects. We have formally defined the attractiveness of a male as the expected value of the surviving offspring produced on mating with the male. The resident mate-choice strategy in a population determines the attractiveness of each type of male. A mutant female is following the best response strategy if her behaviour maximizes the expected attractiveness of the male that she chooses. In this sense attractiveness specifies the mate-choice costs that a female should be prepared to pay to be choosy. The population is evolutionarily stable if resident females are following this best response strategy. Thus an ESS is characterized by the self-consistency of attractiveness: the resident strategy specifies how attractive females should find each male; this strategy is an ESS if and only if resident females are behaving in this way. This phenotypic characterization of evolutionary stability facilitates intuition about sexual selection. It also has enormous advantages over a genetic approach when computing ESS. For example, we have presented a model in which there are 50 types of male. In this model a female's mate-choice strategy specifies a switch time for each type of male, so that it is determined by 50 traits. Genetic models would find it cumbersome to analyse selection in 50 dimensions. By contrast, our approach has no problem in identifying best responses using the power of dynamic optimization techniques such as dynamic programming (applied to a 50-state problem, not a 50-dimension problem).

We have chosen to present our phenotypic approach in the simplest possible case of haploid genetics and phenotypic inheritance of the male trait. This has allowed us to expose the logic of the situation in the clearest way, but the basic logic still holds in other cases. When female choice is determined by diploid genetics, the analysis goes through as before for mutants that are not completely recessive. Completely recessive mutants must be treated differently (e.g. using the approach of Taylor (1990)), as we cannot assume that individuals that are heterozygous for this mutant are rare in determining the projection matrix. When the female choice rule and the male type are both genetically determined, a rare mate-choice allele can be found in $2K$ types of individual: as before there are K types of male but there are now also K types of female because the female carries the male type allele. The projection matrix is thus a $2K$ by $2K$ matrix, but our approach can still be applied. Results depend on whether the expression of the female mate-choice allele can depend on the gene for male type that she is carrying. If such a dependence is possible then models predict that females should put less effort into finding a preferred male if they are already carrying an allele for this male type (J. M. McNamara, M. Marques dos Santos and A. I. Houston, unpublished data). Such complications are easy to deal with in a phenotypic model based on reproductive value calculations.

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APPENDIX A: THE RELATIONSHIP BETWEEN THE GENETIC AND PHENOTYPIC GAMES

To analyse the relationship between the games, we adapt a technique used by Caswell (2001) to look at eigenvalue sensitivity. Consider a resident π population in which the mutant allele π' is rare. At the demographic steady state the ratio of numbers of mutant type i males to mutant females, P'_i is stable and satisfies

$$\mathbf{L}(\pi', \pi) \mathbf{P}'^T = \lambda(\pi', \pi) \mathbf{P}'^T, \quad (\text{A } 1)$$

where \mathbf{P}' denotes the row vector

$$\mathbf{P}' = (P'_1, P'_2, \dots, P'_K, 1). \quad (\text{A } 2)$$

The matrices $\mathbf{L}(\pi', \pi)$ and $\mathbf{L}(\pi, \pi)$ have identical first K columns. Thus by equation (2.6)

$$\mathbf{V}(\pi) [\mathbf{L}(\pi, \pi) - \mathbf{L}(\pi', \pi)] = (0, \dots, 0, W(\pi, \pi) - W(\pi', \pi)). \quad (\text{A } 3)$$

Multiplying both sides of equation (A 3) from the right by \mathbf{P}'^T gives

$$W(\pi, \pi) - W(\pi', \pi) = \mathbf{V}(\pi) [\mathbf{L}(\pi, \pi) - \mathbf{L}(\pi', \pi)] \mathbf{P}'^T. \quad (\text{A } 4)$$

Thus by equations (2.5) and (A 1)

$$W(\pi, \pi) - W(\pi', \pi) = [\lambda(\pi, \pi) - \lambda(\pi', \pi)] \mathbf{V}(\pi) \mathbf{P}'^T. \quad (\text{A } 5)$$

Because $\mathbf{V}(\pi) \mathbf{P}'^T$ is positive we deduce relationship (2.7) of the main text.

APPENDIX B: BEST RESPONSES AND CONTINUOUS STABILITY

For simplicity of exposition we deal with the case of two symmetric male types. In the notation of the text we consider mate-choice strategies of the form $\pi = (0, t_2)$, where t_2 is the switch time at which type 2 males are first accepted. Suppose the resident strategy is $\pi = (0, t_2)$. Then the payoff to a mutant female using mate-choice strategy $(0, s_2)$ in this resident population is $f(s_2) = W((0, s_2), (0, t_2))$. The function f is maximized when the mutant employs the best response rule; i.e. when $s_2 = B(t_2)$. The analysis presented below is based on the plausible assumption that $f(s_2)$ is a unimodal function of s_2 with a unique maximum at $s_2 = B(t_2)$.

Suppose that $B(t_2) > t_2$. By unimodality

$$0 < s_2 < t_2 \Rightarrow W((0, s_2), (0, t_2)) < W((0, t_2), (0, t_2)) \quad (\text{B } 1)$$

and

$$t_2 < s_2 < B(t_2) \Rightarrow W((0, s_2), (0, t_2)) > W((0, t_2), (0, t_2)). \quad (\text{B } 2)$$

Thus by relationship (2.7) of the main text and its analogue with the reverse inequality

$$0 < s_2 < t_2 \Rightarrow \lambda((0, s_2), (0, t_2)) < \lambda((0, t_2), (0, t_2)) \quad (\text{B } 3)$$

and

$$t_2 < s_2 < B(t_2) \Rightarrow \lambda((0, s_2), (0, t_2)) > \lambda((0, t_2), (0, t_2)). \quad (\text{B } 4)$$

In other words, if the resident population is $\pi = (0, t_2)$ and $B(t_2) > t_2$, then there is a selection gradient in the neighbourhood of the resident strategy selecting for higher switch times.

APPENDIX C: THE MODEL WITH 50 MALE TYPES

Males are classified as types 1, 2, ..., 50. If a female mates with a type j male then on average she leaves $N_j = 10 - 0.004j^2$ surviving offspring, half of which are sons. Let

$$v_{ij} = \exp\left(-\frac{(i - 0.8j)^2}{32}\right) \text{ for } i, j = 1, 2, \dots, 50. \quad (\text{C } 1)$$

Then the probability a son is type i is

$$\eta_{ij} = \frac{v_{ij}}{\sum_{k=1}^{50} v_{kj}}. \quad (\text{C } 2)$$

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